

# Yeast - Types of the Basidiomycota Using Cell Wall Sugars and Ribosomal DNA Sequences

HANSJÖRG PRILLINGER<sup>1</sup> & KSENIJA LOPANDIC<sup>2</sup>

**Abstract:** The cell wall carbohydrate composition was correlated with the large subunit rDNA (D1/D2) based phylogeny to estimate its significance in evolution of the Basidiomycota. The majority of investigated isolates showed three main cell wall sugar types: the *Microbotryum*-, the *Ustilago*- and the *Tremella*-type. The *Microbotryum*-type (mannose-glucose-galactose-fucose) corresponded with the subphylum Pucciniomycotina, the *Ustilago*-type (glucose-mannose-galactose) with the Ustilaginomycotina and the *Tremella*-type (glucose-mannose-xylose) with the Agaricomycotina. However, in a number of isolates additional carbohydrates were also identified. A sporadic appearance of rhamnose and xylose within the Microbotryomycetes of the Pucciniomycotina, or glucose-mannose pattern within the Agaricomycetes, and galactose or fucose within the Tremellomycetes of the Agaricomycotina indicated that the cell wall carbohydrate composition characterised rather classes or subclasses than subphyla. The appearance of rhamnose, that is also present in the cell walls of the Taphrinales of the Ascomycota, may indicate a basal position of the Pucciniomycotina in the evolution of the Basidiomycota. This result is in conflict with the D1/D2 based phylogeny, which suggested that the Ustilaginomycotina occupy a basal position in the neighbor-joining tree. The occurrence of the glucose-mannose pattern of the *Saccharomyces*-type of the ascomycetous yeasts and in the highest evolved basidiomycetous yeast isolates (Agaricaceae) from two *Cyphomyrmex* species suggests that the Saccharomycotina are basal in the phylogenetic tree of the Ascomycota. Based on the presence of teliospores, some teleomorphs with CoQ 8 and ribosomal DNA sequences a new class within the Agaricomycotina, the Cystofilobasidiomycetes, was introduced for the *Cystofilobasidium* and *Mrakia* species.

**Zusammenfassung:** Um die Bedeutung der Zellwandzuckerzusammensetzung für die Phylogenie der Basidiomycota zu zeigen, wurde sie mit einem Stammbaum der großen Untereinheit der rDNS (D1/D2) korreliert. Die Mehrheit der untersuchten Isolate zeigte drei charakteristische Zellwandzucker-Typen: der *Microbotryum*-Typ, der *Ustilago*-Typ und der *Tremella*-Typ. Der *Microbotryum*-Typ (Mannose-Glukose-Galaktose-Fukose) korreliert mit dem Subphylum der Pucciniomycotina, der *Ustilago*-Typ (Glukose-Mannose-Galaktose) mit den Ustilaginomycotina und der *Tremella*-Typ (Glukose-Mannose-Xylose) mit den Agaricomycotina. In einer geringeren Anzahl von Isolaten wurden zusätzliche Zucker gefunden. Ein sporadisches Auftreten von Rhamnose und Xylose in den Microbotryomycetes der Pucciniomycotina oder ein Glukose-Mannose Muster innerhalb der Agaricomycotina und Galaktose oder Fukose innerhalb der Tremellomycetes. Dies weist daraufhin, dass die Zellwandzuckerzusammensetzung manchmal auch Klassen oder Unterklassen eher als Subphyla charakterisiert. Das Auftreten von Rhamnose, welche auch in den Zellwänden der Taphrinales innerhalb der Ascomycota sich findet, weist auf eine basale Stellung der Pucciniomycota im Stammbaum der Basidiomycota hin. Dieser Befund ist im Konflikt mit der D1/D2 Phylogenie in der die Ustilaginomycotina eine basale Stellung in einem Neighbor-joining Stammbaum aufweisen. Das Auftreten des Glukose-Mannose Musters (*Saccharomyces*-Typ) bei ursprünglichen Askomyceten-Hefen und in den am höchsten evolvierten Basidiomyceten-Hefen Isolate (Agaricaceae) von zwei *Cyphomyrmex* Arten weist sehr schön darauf hin, dass die Saccharomycotina eine basale Stellung im Stammbaum der Ascomycota aufweisen. Basierend auf der Gegenwart von Teleosporen, das Auftreten von CoQ 8 in einigen Teleomorphen (*Cystofilobasidium*, *Mrakia*) und aufgrund des D1/D2-Stammbaumes wurde eine neue Klasse, die Cystofilobasidiomycetes, innerhalb der Agaricomycotina aufgeführt.

**Keywords:** cell wall sugars; Cystofilobasidiomycetes, 26S rDNA, glucose-mannose-type; *Microbotryum*-type; *Tremella*-type; *Ustilago*-type.

<sup>1</sup>Correspondence to: hansjoerg.prillinger@gmx.at

<sup>1</sup>Ebersbrunn 70, A-3711 Großmeisdorf, Austria; <sup>2</sup>VIBT-BOKU, University of Natural Resources and Applied Life Sciences, Department of Biotechnology, Muthgasse 11, A-1190 Vienna, Austria.

## INTRODUCTION

OBERWINKLER (1977, pers. comm.) has introduced a new interpretation of yeasts as primitive morphological states in the Zygomycota, Ascomycota and Basidiomycota (as “coccal” PRILLINGER 1987a, PRILLINGER et al. 2002, 2003). PRILLINGER et al. (1997a) were able to demonstrate phytopathogenic filamentous (*Ashbya*, *Eremothecium*) and dimorphic fungi (*Holleya*, *Nematosporea*) with needle-shaped ascospores as new members within the Saccharomycetaceae. Since the report of BARTNICKI-GARCIA (1968) on cell wall category, cellular carbohydrate composition has been employed as an important taxonomic criterion in fungi including yeasts. Among the basidiomycetous yeasts three cell wall types occur in the literature using the qualitative and quantitative neutral sugar pattern of purified cell walls:

1. *Microbotryum*-type, with mannose dominant, glucose present, fucose usually present, and rhamnose sometimes present; extracellular amyloid compounds (EAS) are absent (PRILLINGER et al. 1991a, 1993a, 2002, 2011).
2. *Ustilago*-type, with glucose dominant, and mannose and galactose present; EAS absent (PRILLINGER et al. 1990a, 1993a, 2002, 2009, 2011).
3. *Tremella*-type, with glucose dominant, xylose, mannose and galactose present and EAS usually present (PRILLINGER et al. 1991b, 1993a, 1997b, 2002, 2011).

An additional type containing glucose, mannose, xylose and traces of galactose and sometimes fucose in the cell walls was suggested as *Dacrymyces*-type. EAS are usually absent in the members of this group (PRILLINGER et al. 1991b, 1993a, 2011).

The *Microbotryum*-type corresponds with the subphylum Pucciniomycotina, the *Ustilago*-type with the Ustilaginomycotina and the *Tremella*- and *Dacrymyces*-type with the Agaricomycotina (BAUER et al. 2006, BEGEROW et al. 2006, HIBBETT et al. 2007, PRILLINGER et al. 2011). The *Microbotryum*-type and the *Ustilago*-type can only be detected when purified cell walls are analysed (PRILLINGER et al. 1991a, 1993a, 2011, TAKASHIMA et al. 2000). The analysis of carbohydrate composition of whole cells often gives quantitatively different results depending on the age of cultures, affected by the amount of storage carbohydrate such as glycogen in the cells.

Within the Ascomycota there are three genera of importance for the phylogeny of the Basidiomycota. The genera *Saitoella*, *Schizosaccharomyces* and *Taphrina* in the subphylum Taphrinomycotina (Protomycetes in PRILLINGER et al. 2002). The *Schizosaccharomyces* and *Saitoella* species are urease positive and have the cell wall sugars similar to the Ustilaginomycotina: glucose dominant and less amounts of mannose and galactose. The *Taphrina* species are urease positive and have a parasitic, dikaryotic mycelium and a haploid yeast stage like the smut fungi. Fucose is known in the cell wall of *Taphrina vestergrenii*, a sugar characteristic for the *Microbotryum*-type (PRILLINGER et al. 1990b). GOTTSCHALK & BLANZ (1985) have demonstrated that the 5S rRNA of *Taphrina deformans* is characteristic for the Basidiomycota. According to PRILLINGER et al. (1990b, 2002) the Taphrinomycotina (as Protomycetes) are basal in the evolution of the Pezizomycotina and Pucciniomycotina. SAVILE (1955) considered the Taphrinales as primitive rust fungi. No cell wall sugar data are so far available for the Cryptomycococlomycetes, which are basal in a phylogenetic tree of the Pucciniomycotina using LSU rDNA sequences (BAUER et al. 2006).

The main objective of this study was to analyse cell wall carbohydrate composition of additional yeast species, not studied previously, which data are missing in the last edition of “The Yeasts, A Taxonomic Study” (KURTZMAN et al. 2011) and to discuss them in the context of new molecular data on basidiomycetous systematics (AIME et al. 2006, BAUER et al. 2006, BEGEROW et al. 2006, MATHENY et al. 2006, HIBBETT et al. 2007, KURTZMAN et al. 2011, OBERWINKLER 2012 a,b, WEISS et al. 2014).

## MATERIALS AND METHODS

All strains used in this study are listed in Tab. 1.

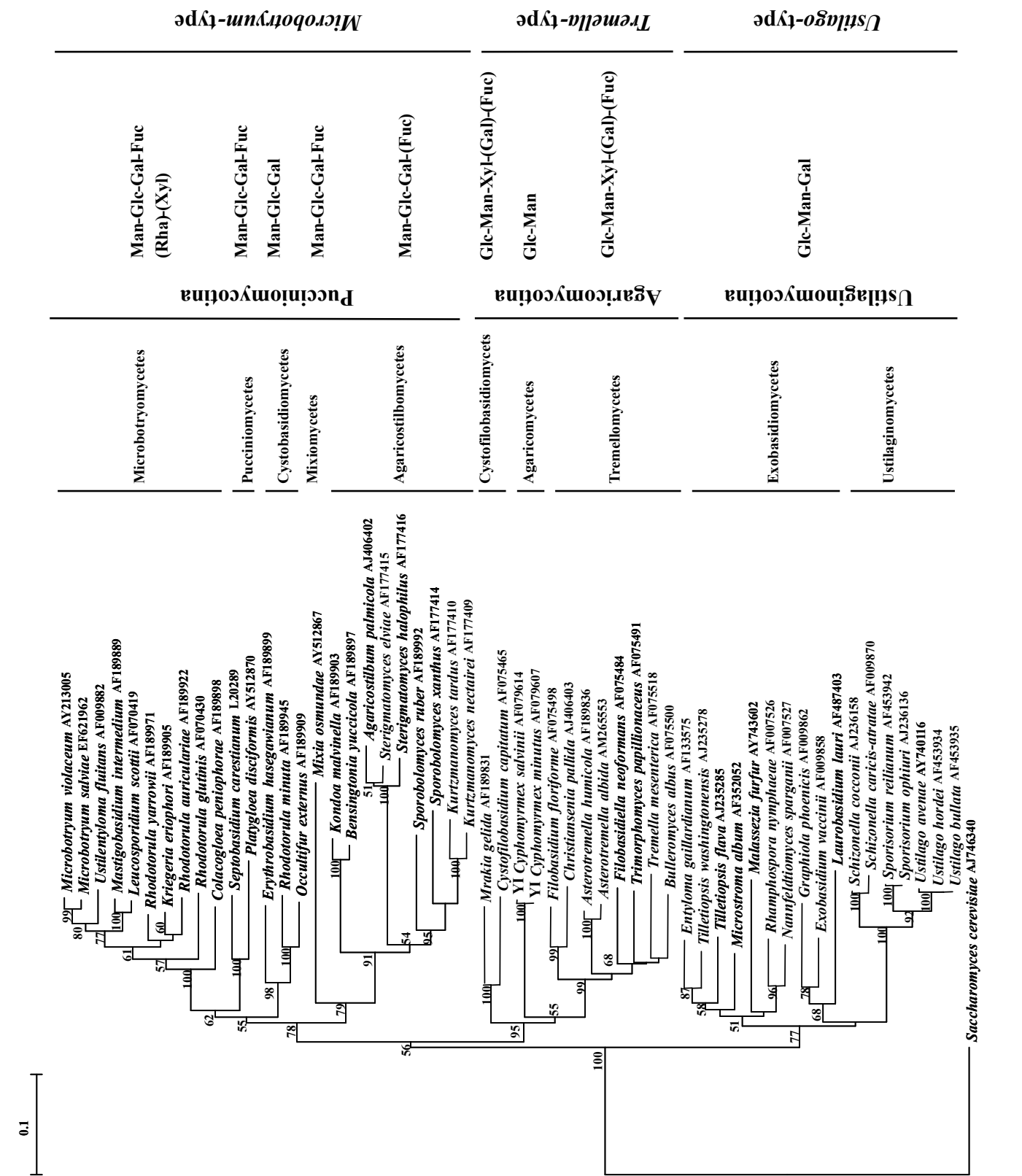
### Phylogenetic analysis of the D1/D2 regions of large-subunit rDNA

Sequences of the D1/D2 regions of 26S rDNA of all strains used in this study were retrieved from GenBank. The strain accession numbers are indicated in Fig. 1. As the sequence of *Microbotryum succisae* is not present in database, the sequence of *M. violaceum*, the type species of the genus *Microbotryum*, is used instead. A pairwise alignment was created using Clustal X (THOMPSON et al. 1997). A neighbor-joining tree was inferred by the program Treecon (VAN DE PEER & DE WACHTER 1994) and genetic distances were calculated using the Kimura two-parameter model. Confidence values for individual branches were determined by bootstrap analyses with 1000 replicates.

Analysis of the cell wall sugar composition: The qualitative and quantitative neutral sugar pattern of purified cell walls was determined as described in DÖRFLER (1990) and LOPANDIC et al. (2005). The cell wall sugars of *Malassezia furfur* were analysed using the post-column fluorescence detection system for reducing sugar analysis by Shimadzu, Japan (Takashima, M., pers. comm.). A brief introduction of that HPLC system can be found in <http://www.shimadzu.com/an/hplc/aplysis/sugar.html>.

## RESULTS AND DISCUSSION

In order to correlate genetic and chemotaxonomic approaches for estimation of the evolutionary relatedness among basidiomycetous yeasts and dimorphic fungi, we studied phylogeny based on partial sequences of the large-subunit rRNA coding gene and the cell wall sugar composition. A neighbor-joining tree constructed on the basis of the D1/D2 sequences supported the three subphyla taxonomic system and demonstrated that the Basidiomycota are divided into the Ustilaginomycotina, the Agaricomycotina and the Pucciniomycotina. The cluster representing the Ustilaginomycotina is supported by 77% bootstrap value and is placed basal in the NJ tree, whereas the Agaricomycotina and the Puciniomycotina seem to be sister groups, although the clade is statistically weakly supported by a bootstrap factor 56%. To similar results came HAMAMOTO & NAKASE (2000), who estimated phylogenetic relationships of 120 basidiomycetous species by 18S rDNA sequences and found that the Ustilaginomycetes (equivalent to the Ustilaginomycotina) might be a common ancestor of the Basidiomycota. The topology of the basidiomy-



**Fig. 1:** Phylogenetic tree showing the relationship of basidiomycetous yeasts and dimorphic fungi on the basis of the large-subunit rDNA D1/D2 sequences. Bootstrap values (>50%) derived from 1000 replicates are shown as percentages. The scale bar represents 0.1 fixed mutation per site. YI = yeast isolates from two *Cyphomyrmex* species; Glc = glucose; Gal = galactose; Fuc = fucose; Man = mannose; Rha = rhamnose; Xyl = xylose; the sugars indicated in parentheses are not characteristic for all fungi of a class (for details see Tables 2-5).

**Table 1:** Investigated strains and their related data.

Species	ACBR Strains	Other designation	Host/l.c./Habitat/other information
<b>PUCCINIOMYCOTINA</b>			
<b>Cystobasidiomycetes</b>			
<i>Erythrobasidium hasegawianum</i> Hamamoto, Sugiyama & Komagata (1991)	HB 62 <sup>T</sup>	CBS 8253 <sup>T</sup>	brewer's yeast, leg. et det. J. Sugiyama Hamamoto, Japan, CoQ 10H <sub>2</sub>
<i>Occultifur externus</i> Sampaio, Bauer & Oberw. (1999)	HB 262 <sup>T</sup>	CBS 8732 <sup>T</sup>	isolated from plant litter, leg. et det. J. P. Sampaio, Portugal, CoQ 10
<i>Rhodotorula minuta</i> (Saito) F.C. Harrison (1928)	HB 477 <sup>T</sup>	CBS 319 <sup>T</sup>	isolated from the atmosphere, Tokyo, Japan, det. J.W. Fell & A. Statzell-Tallman, CoQ 10
<b>Agaricostilbomycetes</b>			
<i>Bensingtonia yuccicola</i> (Nakase & M. Suzuki) Nakase & Boekhout (1988)	HB 419 <sup>T</sup>	CBS 7331 <sup>T</sup> JCM 6251 <sup>T</sup>	old fallen leaf of <i>Yucca</i> , sp. leg. et det. R.J. Bandoni, Vancouver, Canada, CoQ 9
<i>Kurtzmanomyces nectairei</i> Rodrigues de Miranda, Y. Yamada, Itoh, Kawasaki, Banno & Nakase (1988)	HB 106 <sup>T</sup>	CBS 6405 <sup>T</sup>	isolated from cheese of St. Nectaire, France, CoQ 10
<i>Kurtzmanomyces tardus</i> Gimenez-Jurado & van Uden (1990)	HB 268 <sup>T</sup>	CBS 7421 <sup>T</sup>	from contaminated demineralized water, Oeiras Portugal; leg. T. Placido, CoQ 10
<i>Sporobolomyces ruber</i> (Nakase, Okada & Sugiyama) Boekhout (1991)	HB 317 <sup>T</sup>	CBS 7512 <sup>T</sup> JCM 6884 <sup>T</sup>	ex dead leaf of <i>Vitis ficifolia</i> var. <i>lobata</i> , leg. et det. T. Nakase, Japan, CoQ 10
<i>Sporobolomyces xanthus</i> (Nakase, Okada & Sugiyama) Boekhout (1991)	HB 316 <sup>T</sup>	CBS 7513 <sup>T</sup> JCM 6885 <sup>T</sup>	ex dead leaf of <i>Acer rufrinerve</i> , leg. et det. T. Nakase Japan, CoQ 10
<i>Sterigmatomyces elviae</i> Sonck & Yarrow (1969)	HB 104 <sup>T</sup>	CBS 5922 <sup>T</sup>	isolated by E. Tunnela from groin of man with seborrheic eczema in Finland, CoQ 10
<i>Sterigmatomyces halophilus</i> Fell (1966)	HB 100 <sup>T</sup>	CBS 4609 <sup>T</sup>	isolated by B. Ojeda from air, Virginia Key, Florida, USA, CoQ 10
<b>Microbotryomycetes</b>			
<i>Kriegeria eriophori</i> Bresadola (1891)	HB 263	RB 1031	leg. et det. R. Bauer, Germany, CoQ 10
<i>Mastigobasidium intermedium</i> Golubev (1999)	HB 417 <sup>T</sup>	CBS 7226 <sup>T</sup>	ex dead leaf of <i>Oryza sativa</i> , leg. et det. V.I. Golubev, CoQ 9
<i>Microbotryum salviae</i> (Ferraris) Kemler, M. Lutz, Oberw. & Begerow (2007)	HB 315	BBA 67487	<i>Salvia pratensis</i> , leg. et det. G. Hagedorn, Tübingen, Spitzberg, Germany, CoQ 10
<i>Microbotryum succisae</i> (Magnus) R. Bauer & Oberw. (1997)	HB 313	BBA 67910	ex <i>Succisa pratensis</i> , leg. et det. G. Hagedorn, Tübingen, Germany, CoQ 10
<i>Rhodotorula auriculariae</i> (Nakase) Rodrigues de Miranda & Weijman (1988)	HB 413 <sup>T</sup>	CBS 6379 <sup>T</sup>	fruiting body of <i>Auricularia auricular-judae</i> , leg. et det. J.W. Fell & A. Statzell-Tallman, USA
<i>Rhodotorula glutinis</i> (Fresenius) F.C. Harrison (1928)	HB 476 <sup>T</sup>	CBS 20 <sup>T</sup>	isolated by N. Pringsheim (Berlin) from the atmosphere, CoQ 10
<i>Rhodotorula yarrowii</i> (A. Fonseca & van Uden) Boekhout, Fell, Fonseca, Prillinger & Roeljmans (2000)	HB 705 <sup>T</sup>	CBS 7417 <sup>T</sup>	isolated from decaying mushroom by Fonseca & van Uden, det. by T. Boekhout, CoQ 9
<b>Pucciniomycetes</b>			
<i>Platygløea disciformis</i> (Fr.) Neuhoﬀ (1936)	HB 267		leg. et det. F. Oberwinkler, Tübingen, Germany
<b>Mixiomycetes</b>			
<i>Mixia osmundae</i> (Nishida) C.L. Kramer (1959)	HB 749	CBS 9802 JCM 22182 IAM 14324	isolated from fronds of <i>Osmunda japonica</i> by K. Ando, in Sezawa, Nakakawane-cho, Haibara-gun, Shizuoka-ken, Japan, CoQ 10

Table 1: continued.

Species	ACBR Strains	Other designation	Host/l.c./Habitat/other information
<b>USTILAGINOMYCOTINA</b>			
<b>Exobasidiomycetes</b>			
<i>Malassezia furfur</i> (Robin) Baillon (1889)	no data	CBS 7019 <sup>T</sup> JCM 9199 <sup>T</sup>	isolated from <i>Pityriasis versicolor</i> from trunk of a 15-year-old girl, Finland, CoQ 9
<i>Nannfeldtiomyces sparganii</i> Vánky (1981)	HB 304	BBA 68271	ex <i>Sparganium</i> , leg. et det. G. Hagedorn, Tübingen, Germany, CoQ 10
<i>Rhamphospora nymphaeae</i> D. Cunningham (1988)	HB 405	RB 862	leg. et det. R. Bauer, Tübingen, Germany, CoQ 10
<b>Ustilaginomycetes</b>			
<i>Schizonella caricis-atratae</i> Prillinger, Wuczowski & Lopandic (2009)	HB 3 <sup>T</sup>	CBS 123477 <sup>T</sup>	ex <i>Carex atrata</i> , collected at the top of the mountain “Schneealpe” Austria, Styria, leg. et det. H. Prillinger, CoQ 10
<i>Schizonella cocconii</i> (Morini) Liro (1938)	HB 112		ex <i>Carex halleriana</i> with <i>Anthracoidea</i> , sp., leg. et det. H. Prillinger, Perchtoldsdorf, Austria, CoQ 10
<i>Sporisorium ophiuri</i> (Henn.) Vánky (1986)	HB 19		ex <i>Rottboellia cochinchinensis</i> plant, CoQ 10
<i>Sporisorium reilianum</i> (J.G. Kühn) Langdon & Full. (1978)	HB 303		head smut on maize, leg. et det. J. Kronstad, University of British Columbia, Canada, CoQ 10
<i>Ustilago avenae</i> (Pers.) Rostr. (1890)	HB 299		ex <i>Avena sativa</i> , leg. et det. J. Kronstad, University of British Columbia, Canada, CoQ 10
<i>Ustilago bullata</i> Berkeley (1855)	HB 296		ex <i>Bromus tectorum</i> , leg. et det. J. Kronstad, University of British Columbia, Canada, CoQ 10
<i>Ustilago hordei</i> (Pers.) Lagerh. (1889)	HB 297		ex <i>Hordeum vulgare</i> , leg. et det. J. Kronstad, University of British Columbia, Canada, CoQ 10
<b>AGARICOMYCOTINA</b>			
<b>Tremellomycetes</b>			
<i>Asterotremella albida</i> (Ramirez Gomez) Prillinger, Lopandic & Sugita (2007)	HB 81 <sup>T</sup>	CBS 10411 <sup>T</sup>	yeast isolate from <i>Asterophora lycoperdoides</i> , Pirkensee near Regensburg, Bavaria, Germany, leg. et det. H. Prillinger, CoQ 9
<i>Asterotremella humicola</i> (Daszewska) Prillinger, Lopandic & Sugita (2007)	HB 370 <sup>T</sup>	CBS 571 <sup>T</sup>	isolated from heath soil in Switzerland, CoQ 9
<i>Christiansenia pallida</i> Hauerslev (1969)	HB 91	FO 36413	parasitic on <i>Phanerochaete</i> , leg. et det. F. Oberwinkler, Germany
<i>Filobasidiella neoformans</i> Kwon-Chung (1975)	HB 420 <sup>T</sup>	CBS 6885 <sup>T</sup>	lesion on bone of man, CoQ 10
<b>Agaricomycetes</b>			
Yeast isolate from <i>Cyphomyrmex salvini</i> (Agaricaceae)	HB 666		isolated by U.G. Mueller ex leaf-cutting ants
Yeast isolate from <i>Cyphomyrmex minutus</i> (Agaricaceae)	HB 667		isolated by U.G. Mueller ex leaf-cutting ants

ACBR= Austrian Center of Biological Resources and Applied Mycology, Vienna, Austria; CBS=Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; JCM= Japan Collection of Microorganisms, Wako, Tsukuba, Japan; FO and RB= herbarium and culture collection of Franz Oberwinkler and Robert Bauer, University of Tübingen, Germany; BBA=Federal Biological Research-Center for Agriculture and Forestry, Berlin, Germany. CoQ data according to KURTZMAN et al. (2011), Molnár (pers. comm.) and PRILLINGER et al. (1990a). Superscript indicates type-strain.



cetous fungi was always a matter of debate, and even SWANN & TAYLOR (1993) indicated that the small-subunit rRNA (18S) gene sequence is not able to resolve the relationships among the three classes (equivalent to subphyla) of Basidiomycota. In a subsequent report, the same authors (SWANN & TAYLOR 1995), studying phylogeny based on 18S rRNA gene sequences of 35 yeast-producing basidiomycetes, indicated that the Urediniomycetes (equivalent to the Pucciniomycotina) may have a basal position, whereas the Ustilaginomycetes and Hymenomycetes (equivalent to the Agaricomycotina) appear as sister groups. The basal position of the Pucciniomycotina was also suggested in our previous studies by comparison of physiological, chemotaxonomic and genetic data (PRILLINGER et al. 1990a, 1990b, 1991a, 1991b, 1993a, 2000, 2002), where dominance of the mannose and partial existence of the rhamnose (a characteristic sugar of the Taphrinales in the Taphrinomycotina) indicated a link between the Basidio- and Ascomycotina. The relationship between cell wall sugar component and 18S rDNA based phylogeny in the Ascomycotina was shown by SCHWEIGKOFER et al. (2002) and LOPANDIC et al. (2005) and in the Basidiomycotina by PRILLINGER et al. (2000, 2002) and TAKASHIMA et al. (2000). Differently from HIBBETT et al. (2007) in our phylogenetic tree (Fig. 1) the Tremellomycetes are not homogenous. The Agaricomycetes cluster between the dipartite Tremellomycetes clade. Similar to our tree, FELL (2011) and BANDONI & BOEKHOUT (2011) showed that Cystofilobasidiales are only distantly related to Tremellales and Filobasidiales within the Tremellomycetes. We therefore introduce the new class, the Cystofilobasidiomycetes for *Cystofilobasidium* and *Mrakia* species having a Co Q 8 and the presence of teliospores.

Although our previous results (PRILLINGER et al. 1990a, 1990b, 1991a, 1991b, 1993a) suggested a strong correlation between the cell wall carbohydrate patterns and three subphyla in the 18S rDNA-based phylogenetic tree (SWANN & TAYLOR 1995, PRILLINGER et al. 2000, 2002), results of the present study clearly show that the Basidiomycota are characterised by at least four cell wall carbohydrate profiles (Tables 2–5). All representatives of the Ustilaginomycotina except *Malassezia furfur* (only glucose) are characterised by the cell wall sugar pattern glucose-mannose-galactose (Fig. 1, Table 3). Glucose is present in the range from 70% up to >95%, and mannose and galactose from 12 up to 39% and 1% up to 16% respectively. Similarly, the Tremellomycetes of the Agaricomycotina contain a dominant amount of glucose (>60%) and a significantly lower level of mannose (4%–22%). Differently from the Ustilaginomycotina, the cell walls of all investigated strains of the Tremellomycetes and Cystofilobasidiomycetes contain low amount of xylose (1%–12%), and galactose and fucose are detected sporadically (Fig. 1, Table 4). Only two representatives of the Agaricomycetes, the yeast isolates from leaf-cutting ants *Cyphomyrmex minutus* and *C. salvinii* are characterised by a glucose-mannose pattern, a new carbohydrate profile not described within the Basidiomycota so far (Fig. 1, Table 5). The members of the subphylum Pucciniomycotina are characterised by a significant amount of mannose (>55%) in comparison to glucose (10%–35%) and galactose (1%–16%). Presence of fucose in the cell walls of the Microbotryomycetes, Pucciniomycetes and Mixiomycetes distinguishes them from the Agaricostilbomycetes and the Cystobasidiomycetes, where this sugar appears sporadically or is completely absent. In the Agaricostilbomycetes *Sterigmatomyces halophilus* contains only

mannose as dominant sugar and glucose. Rhamnose also appears sporadically in the Microbotryomycetes, while the cell wall of *Rhodotorula yarrowii* are characterized by the presence of xylose in addition to the other sugars (Fig. 1, Table 2). These results suggest that some carbohydrate patterns may characterize rather classes or subclasses than the subphyla, as it is clearly shown by the Agaricomycetes and the Tremellomycetes. Presence of rhamnose within the Microbotryomycetes of the Pucciniomycotina, as well as the glucose-mannose pattern in two yeast isolates from two *Cyphomyrmex* species within the Agaricomycotina, may have an importance in evolutionary history of the basidiomycetous fungi. The sporadic presence of rhamnose in the Microbotryomycetes and fucose in *Taphrina vestergronii* suggests that the Pucciniomycotina have evolved from the Taphrinomycotina (as Protomycetes in PRILLINGER et al. 2000, 2002 and LOPANDIC et al. 2005). The presence of the glucose-mannose pattern at the beginning of ascomycetous yeasts (*Saccharomyces*-type; PRILLINGER et al. 1990b, 1993a) and in the most highly evolved two agaricoid yeast isolates from the *Cyphomyrmex* species suggests that the Saccharomycotina occupy a basal position in the Ascomycota as suggested by PRILLINGER et al. (2000, 2002).

### Yeasts and dimorphic fungi belonging to the *Microbotryum*-type:

**Cystobasidiomycetes:** The cell walls are characterized by the absence of fucose (Fig. 1, Table 2; Bauer et al. 2006, Takashima et al. 2000). Takashima et al. (2000) mentioned the absence of fucose only in the Erythrobasidiales. This is confirmed in the present investigation (Table 2). According to ribosomal DNA sequences (SAMPAIO & OBERWINKLER 2011a) the species *Occultifurax externus* and *Rhodotorula minuta* are placed in the Cystobasidiales. BAUER et al. (2006) suggested the family Cystobasidiaceae for both species (Fig. 1). The qualitative and quantitative neutral sugar pattern of both species is closely related (Table 2). *Rhodotorula* species of the Cystobasidiomycetes were placed in the new genus *Cystobasidium* (*R. minuta* = *C. minutum*; YURKOV et al. 2015). *Erythrobasidium hasegawianum* is placed in a second order the Erythrobasidiales of the Cystobasidiomycetes (Fig. 1; BAUER et al. 2006, HAMAMOTO 2011).

**Agaricostilbomycetes:** It is possible that the Agaricostilbomycetes have to be separated into two classes in the future, but at the moment, a separation appears to be premature (Fig. 1). In the Agaricostilbales the following species can be included (Fig. 1; BOEKHOUT et al. 2011): *Bensingtonia yuccicola* (Kondooaceae, see below), *Agaricostilbum palmicola* forms small stilboid basidiocarps on dead, attached or fallen palm litter, *Sterigmatomyces elviae*, *St. halophilus* (Agaricostilbaceae); *Kurtzmanomyces tardus*, *K. nectairei* (Chionosphaeraceae), *Sporobolomyces ruber* and *Sp. xanthus* (Chionosphaeraceae). In our cell wall sugar analysis the *Kurtzmanomyces* and *Sterigmatomyces* species did not have fucose (Table 2). *Sterigmatomyces halophilus* has only mannose and glucose in its cell wall. Dominant amounts of mannose suggest a placement in the *Microbotryum*-type. The genus *Sporobolomyces* in its current concept is highly polyphyletic. Species belong to four different lineages of the Pucciniomycotina (HAMAMOTO et al. 2011). The genus *Kondoa* was introduced to accommodate a single taxon, *Kondoa malvinella*, which was transferred from the teliospore-forming genus *Rhodospodidium* on the basis of pronounced differences in partial SSU and LSU rRNA sequences with *Rh. toruloides*, the type species of the lat-

**Table 2:** Yeasts and dimorphic fungi of the *Microbotryum*-type belonging to the Pucciniomycotina (AIME et al. 2006; BAUER et al. 2006). Because the molecular taxonomy of the genera *Agaricostilbum*, *Kondoa*, *Leucosporidium*, *Ustilentyloma*, *Septobasidium* and *Colacogloea* was not studied previously by PRILLINGER et al. (1991a, 1993a), these genera were included in the present investigation.

Species	Strain	Cell wall sugars mol%					
		GLC	MAN	GAL	XYL	FUC	RHA
<b>Cystobasidiomycetes</b>							
<i>Erythrobasidium hasegawianum</i>	HB 62 <sup>T</sup>	28	70	2	-	-	-
<i>Occultifur externus</i>	HB 262 <sup>T</sup>	23	74	3	-	-	-
<i>Rhodotorula minuta</i>	HB 477 <sup>T</sup>	25	71	4	-	-	-
<b>Agaricostilbomycetes</b>							
<i>Agaricostilbum palmicola</i>	HB 534	23	74	2	-	1	-
<i>Bensingtonia yuccicola</i>	HB 419 <sup>T</sup>	27	70	1	-	1	-
<i>Kurtzmanomyces nectairei</i>	HB 106 <sup>T</sup>	12	87	0.4	-	-	-
<i>K. tardus</i>	HB 268 <sup>T</sup>	17	81	2	-	-	-
<i>Sterigmatomyces elviae</i>	HB 104 <sup>T</sup>	19	80	1	-	-	-
<i>St. halophilus</i>	HB 100 <sup>T</sup>	39	61	-	-	-	-
<i>Sporobolomyces ruber</i>	HB 317 <sup>T</sup>	14	75	6	-	5	-
<i>Sp. xanthus</i>	HB 316 <sup>T</sup>	12	83	2	-	3	-
<i>Kondoa malvinella</i>	CBS 6082 <sup>T</sup>	25	69	4	-	1	-
<b>Microbotryomycetes</b>							
<i>Mastigobasidium intermedium</i>	HB 417 <sup>T</sup>	15	80	3	-	2	-
<i>Leucosporidium scottii</i>	HB 616 <sup>T</sup>	29	60	7	-	4	-
<i>Microbotryum salviae</i>	HB 315	10	59	7	-	24	-
<i>M. succisae</i>	HB 313	10	45	12	-	33	-
<i>Ustilentyloma fluitans</i>	RB 900	12	74	5	-	8	-
<i>Rhodotorula auriculariae</i>	HB 413 <sup>T</sup>	16	79	1	-	1	3
<i>R. glutinis</i>	HB 462 <sup>T</sup>	20	78	1	-	1	-
<i>R. yarrowii</i>	HB 705 <sup>T</sup>	20	58	2	5	2	13
<i>Kriegeria eriophori</i>	HB 263	22	49	16	-	9	4
<i>Colacogloea peniophorae</i>	HB 535	16	60	11	-	3	10
<b>Pucciniomycetes</b>							
<i>Platygløea disciformis</i>	HB 267	23	73	1	-	1	-
<i>Septobasidium carestianum</i>	HB 614	26	60	10	-	5	-
<b>Mixiomycetes</b>							
<i>Mixia osmundae</i>	HB 749	35	55	7	-	2	-

ter genus (YAMADA et al. 1998). Species of the genus *Kondoa* are placed in the family Kondooaceae (Fig. 1; BAUER et al. 2006).

**Microbotryomycetes:** In the order Microbotryales (Fig. 1) family Microbotryaceae *Microbotryum salviae* and *M. succisae* are accommodated. *Sphacelotheca hydropiperis* (PRILLINGER et al. 1991a) in addition is also a member of the Microbotryales (BAUER et al. 2006). For *Ustilentyloma fluitans* the family Ustilentylomataceae was suggested (BAUER et al. 2006). The Spo-

ridiobolales (Sporidiobolaceae) contain *Rhodotorula glutinis* (Fig. 1), and *Rhodospiridium diobovatum* and *Rh. toruloides* from PRILLINGER et al. (1991a). In contrast *Rh. malvinellum* from PRILLINGER et al. (1991a) clusters within the Agaricostilbomycetes (TAKASHIMA et al. 2000) family Kondooaceae. *Sporobolomyces roseus*, *Sp. salmonicolor* and *Sp. tsugae* from PRILLINGER et al. (1991a) are found in the Microbotryomycetes (the order so far is unknown). *Leucosporidium scottii* and *Mastigobasidium*

**Table 3:** Dimorphic fungi of the *Ustilago*-type belonging to the Ustilaginomycotina (BEGEROW et al. 2006). Because the molecular taxonomy of the genera *Exobasidium*, *Tilletiopsis*, *Microstroma*, *Laurobasidium* (as *Exobasidium lauri*) and *Graphiola* was not studied previously by PRILLINGER et al. (1990a, 1993a), the genera were included in the present investigation.

Species	Strain	Cell wall sugars mol%					
		GLC	MAN	GAL	XYL	FUC	RHA
<b>Exobasidiomycetes</b>							
<b>Doassansiales</b>							
<i>Nannfeldtiomyces sparganii</i>	HB 304	87	2	11	-	-	-
<i>Rhamphospora nymphaeae</i>	HB 405	85	0,4	14	-	-	-
<b>Exobasidiales</b>							
<i>Exobasidium vacinii</i>	HB 243	82	3	14	-	-	-
<i>Laurobasidium lauri</i>	Pr 1989	71	12	18	-	-	-
<b>Graphiolales</b>							
<i>Graphiola phoenicis</i>	HB 255	82	12	7	-	-	-
<b>Entylomatales</b>							
<i>Entyloma gailardianum</i>	HB 602	79	3	18	-	-	-
<i>Tilletiopsis washingtonensis</i>	HB 590	89	2	10	-	-	-
<b>Georgefischeriales</b>							
<i>Tilletiopsis flava</i>	HB 592	91	4	5	-	-	-
<b>Microstromatales</b>							
<i>Microstroma album</i>	HB 799	90	6	3	-	-	-
<b>Ustilaginomycetes</b>							
<b>Ustilaginales</b>							
<i>Schizonella caricis-atratae</i>	HB 3 <sup>T</sup>	88	5	7	-	-	-
<i>Sch. cocconii</i>	HB 112	93	2	5	-	-	-
<i>Sporisorium ophiuri</i>	HB 19	96	2	2	-	-	-
<i>Sp. reilianum</i>	HB 303	96	1	3	-	-	-
<i>Ustilago avenae</i>	HB 302	71	27	2	-	-	-
<i>U. bullata</i>	HB 296	72	25	3	-	-	-
<i>U. hordei</i>	HB 297	84	13	3	-	-	-

*intermedium* are found in the Leucosporidiales (Fig. 1; Leucosporidiaceae; BAUER et al. 2006). *Rhodotorula auriculariae* and *R. yarrowii* have no distinct order and are in the *Leucosporidium antarcticum* clade (BOEKHOUT et al. 2011) with possible relationships to the Kriegeriales (compare Fig 1). The genus *Rhodotorula* is heterogenous; species can be found in the Cy-stobasidiomycetes and the Microbotryomycetes as well as in the Ustilaginomycotina (Ustilaginomycetes: *R. acheniorum*; Exo-basidiomycetes: *R. bacarum* and *R. phylloplana*). *Rhodotorula yarrowii* is a remarkable fungus; it is the only one yeast which

contains xylose in its cell wall (BOEKHOUT et al. 2000). Dominant amounts of mannose in the cell wall, however, point to a position in the *Microbotryum*-type. High amounts of rhamnose in addition suggest affinities to the *Protomyces*-type (PRILLINGER et al. 1990b). Smaler amounts of rhamnose occur in *Rhodotorula auriculariae* and *Kriegeria eriophori* (Table 2). The genus *Kriegeria* is placed in the family Kriegeriaceae, order Kriegeriales (Fig. 1; TOOME et al. 2013). The genus *Colacogloea* was erected to accommodate species of the “simple”-pored mycoparasitic, dimorphic heterobasidiomycetes with transversely septate basi-



**Table 4:** Yeasts and dimorphic fungi of the *Tremella*-type belonging to the Agaricomycotina, Tremellomycetes (WEISS et al. 2014) and the new class Cystofilobasidiomycetes. Because the molecular taxonomy of the genera *Trimorphomyces*, *Mrakia*, *Tremella*, *Filobasidium*, *Cystofilobasidium* and *Bulleromyces* (as *Bullera*) was not investigated previously by PRILLINGER et al. (1991b), these are included in the present publication.

Species	Strain	Cell wall sugars mol%					
		GLC	MAN	GAL	XYL	FUC	RHA
<b>Tremellomycetes</b>							
<b>Trichosporonales</b>							
<i>Asterotremella albida</i>	HB 81	83	10	-	6	-	-
<i>A. humicola</i>	CBS 571	84	10	-	3	-	-
<b>Filobasidiales</b>							
<i>Christiansenia pallida</i>	HB 91	62	22	-	12	4	-
<i>Filobasidium floriforme</i>	HB 79 <sup>T</sup>	88	7	1	3	-	-
<b>Tremellales</b>							
<i>Filobasidiella neoformans</i>	HB 420 <sup>T</sup>	82	14	0.5	3	-	-
<i>Tremella mesenterica</i>	HB 659	91	4	1	4	-	-
<i>Trimorphomyces papilionaceus</i>	HB 676	84	8	-	7	-	-
<i>Bulleromyces albus</i>	DSM 70002	86	9	1	3	-	-
<b>Cystofilobasidiomycetes</b>							
<b>Cystofilobasidiales</b>							
<i>Cystofilobasidium capitatum</i>	HB 65	93	5	-	1	1	-
<i>Mrakia gelida</i>	CBS 5272	80	9	-	6	4	-

dia and colacosomes (OBERWINKLER et al. 1990). High amounts of rhamnose suggest affinities to the *Protomyces*-type (PRILLINGER et al. 1990b). *Colacogloea peniophorae* is placed in the order Heterogastridiales family Heterogastridiaceae (Fig. 1; BAUER et al. 2006, OBERWINKLER 2012 a,b).

**Pucciniomycetes:** *Platyglaea disciformis* (Fig. 1) is accommodated in the order Platyglaeales family Platyglaeaceae. The Platyglaeales comprise phytoparasites mainly on stems and leaves (BAUER et al. 2006). *Septobasidium carestianum* (Fig. 1) is placed in the order Septobasidiales family Septobasidiaceae (BAUER et al. 2006). The Septobasidiales are parasites on scale insects (COUCH 1938).

**Mixiomycetes:** Main characteristics are multinucleate hyphae, multiple spores produced simultaneously on sporogenous cells (NISHIDA et al. 1995, 2011, BAUER et al. 2006). There is only one species *Mixia osmundae* (Fig. 1) in the family Mixiaceae.

**Yeasts and dimorphic fungi belonging to the *Ustilago*-type:**

The thorough investigation of ultrastructural characters ended in a complete revision of the classification of the Usti-

laginomycotina (BAUER et al. 1997). The Ustilaginomycotina comprises not only smut fungi but also nonteliosporic plant parasites such as *Graphiola*, *Exobasidium*, *Microstroma* and a few smaller genera (Fig. 1, Table 3; PRILLINGER et al.1990a, 1993a, 2002, BAUER et al. 2006). A group of human and animal pathogens, Malasseziales, is placed within Ustilaginomycotina as well (BEGEROW et al. 2000). Presently three classes are accepted: Entorrhizomycetes, Exobasidiomycetes and Ustilaginomycetes (BEGEROW et al. 2006).

**Exobasidiomycetes:** This class represents the sister group of Ustilaginomycetes (BEGEROW et al. 1997). The Exobasidiomycetes form local interaction zones (BAUER et al. 2006), they are predominantly holobasidiolate and consists of teliosporic Doassansiales, Entylomatales, Georgefischeriales and Tilletiales, nonteliosporic Ceraceosorales, Exobasidiales and Microstromatales, as well as the anamorphic Malasseziales. In comparison to Ustilaginomycetes the ecology of Exobasidiomycetes is highly diverse. *Nannfeldtiomyces sparganii* and *Rhamphospora nymphaeae* are placed in the order Doassansiales (Fig. 1). Species of *Nannfeldtiomyces* produce spore balls in leaves or stems of aquatic or paludal plants (Sparganiaceae, VÁNKY 1987). The monotypic genus *Rhamphospora* produces single spores on species of Nymphaeaceae (VÁNKY 1987); it is placed in the family

**Table 5:** Dimorphic fungi of the glucose-mannose-type belonging to the Agaricomycotina, Agaricomycetes.

Species	Strain	Cell wall sugars mol%					
		GLC	MAN	GAL	XYL	FUC	RHA
<b>Agaricomycetes</b>							
<b>Agaricaceae</b>							
Y.i. <i>Cyphomyrmex minutus</i>	HB 667	98	2	-	-	-	-
Y.i. <i>C. salvinii</i>	HB 666	97	3	-	-	-	-

Y. i.: Yeast isolate

Rhamphosporaceae (OBERWINKLER 2012 a, b). Included in the Exobasidiales (Fig. 1) are *Exobasidium vacinii* (family: Exobasidiaceae), *Laurobasidium lauri* (family: Cryptobasidiaceae) and *Graphiola phoenicis* (family: Graphiolaceae). The family Exobasidiaceae can also be distinguished from the family Cryptobasidiaceae by cell wall sugars (Table 3). *E. vaccinii* is parasitic on *Vaccinium vitis-idea*; *L. lauri* occurs on stems of laurels with large (12 cm) clavarioid galls and Graphiolaceae are parasites of palms. During differentiation of the cylindrical basidiocarp, the epidermis ruptures and globose basidia are produced in chains by disarticulation of sporogenous hyphae within the basidiocarps. The passively released basidiospores arise laterally on basidia (OBERWINKLER et al. 1982). Based on this distinct morphology OBERWINKLER (2012 a, b) postulates the order Graphiolales for the Graphiolaceae. Basidia of *L. lauri* are gastroid. Ten different species of *Exobasidium* were investigated by PRILLINGER et al. (1990a). The members of the Entylomatales are morphologically very similar. So far this group comprises only species of *Entyloma* occurring on dicots with holobasidia and some *Tilletiopsis* species (Fig. 1). Former *Entyloma* species occurring on monocots were transferred to several genera of the Georgefischeriales (BAUER et al. 2001a, Begerow et al. 2006). The species are not easy to distinguish from each other (VÁNKY 1994). They form a *Tilletiopsis*-like pseudohyphal anamorph that usually produces ballistoconidia (BOEKHOUT 1991). *Entyloma gaillardianum* occurs on *Gaillardia aristata*. *Entyloma dactylis* on *Agrostis* sp. (a monocot) was transferred in the genus *Jamesdicksonia* as *J. dactylis* in the family Georgefischeriaceae of the Georgefischeriales by BAUER et al. (2001a). This is also supported by a significantly higher glucose content in purified cell walls (PRILLINGER et al. 1993a). The genus *Tilletiopsis* is polyphyletic (Fig. 1; BOEKHOUT 2011). *T. washingtonensis* was isolated from a fruiting body of *Asterophora lycoperdoides*. *T. washingtonensis* is the type species of the genus *Tilletiopsis*. *T. flava* (Fig. 1) is a member of the Georgefischeriales; it is included in the family Tilletiariaceae. *T. flava* can be differentiated from both *T. fulvescens* and *T. minor* by its inability to grow on galactose, lactose, melezitose, and erythritol (BOEKHOUT 1991). *Microstroma album* (Fig. 1) is found on *Juglans* and can be found in the order Microstromatales (Table 3). The Georgefischeriales cannot be distin-

guished from the Microstromatales by cell wall sugars (Table 3).

Anamorphic Malasseziales: One strain of *Malassezia furfur* (Fig. 1) was analysed for cell wall sugars (Takashima, M., pers. comm.). There were problems in preparing cell walls, because cells aggregated very heavily and mechanical disruption with glass beads was difficult. There was no confidence whether or not cell wall was correctly purified. In the analysis very high amounts of glucose (more than 98%) appeared. Mannose and galactose were below 1% and could not be identified unequivocally. Based on the high glucose concentration, however, these data may indicate that the Malasseziales occupy a very derived position within the Ustilaginomycotina.

**Ustilaginomycetes:** The majority of Ustilaginomycotina belong to this class. It is a teliosporic, dimorphic and gastroid group characterized by the presence of enlarged interaction zones (BAUER et al. 2006). Ustilaginomycetes is dichotomous, consisting of the predominantly holobasidiate Urocystales and predominantly phragmobasidiate Ustilaginales. The last order comprises the majority of smut fungi including the large genera *Ustilago* and *Sporisorium* (Table 3). Both genera are included in the family Ustilaginaceae. Prillinger et al. (1990a, 1993a) and BAUER et al. 2001b) have shown by cell wall sugar analysis, ultrastructural and molecular data that “true *Ustilago* species” occur only on grasses (Poaceae). Several molecular studies have shown that the separation of *Ustilago* and *Sporisorium* is difficult based on previously used characters (STOLL et al. 2003, 2005). In our cell wall sugar analysis (Table 3) the two *Sporisorium* species *Sp. ophiuri* and *Sp. reilianum* are closely related (Fig. 1) and distinct from *Ustilago avenae*, *U. bullata* and *U. hordei*. In a previous study (PRILLINGER et al. 1990a), *Sp. destruens comes* close to *Sp. ophiuri* and *Sp. reilianum*. According to STOLL et al. (2005) *Sp. ophiuri* and *Sp. reilianum* represent *Sporisorium* 1 species, whereas *Sp. destruens* is a *Sporisorium* 2 species. Cell wall sugars can therefore not be used to separate *Sporisorium* 1 and *Sporisorium* 2 species. Only *Sp. transfixum*, *Sp. cenchri* and *Sp. puellare* can not be distinguished from *U. hordei* (PRILLINGER et al. 1990a, 1993a). In a molecular investigation, BEGEROW et al. (2006) showed that *U. avenae*, *U. bullata*, *U. hordei* (Fig. 1), *U. tritici*, *U. cynodontis* and *U. striiformis* form a homogenous clade, whereas *Ustilago maydis*, *U. davisii* and *U. trichophora*

are placed in different groups. *U. maydis* clusters with *Sporisorium* species (STOLL et al. 2003, 2005, compare cell wall sugars in Prillinger et al. 1990a). OBERWINKLER (2012 b) suggested the old Brefeld' genus *Mycosarcoma* for *U. maydis*. According to STOLL et al. (2003, 2005) *Sporisorium* species occur on a subfamily of the Poaceae, the Panicoide and *Ustilago* species on the subfamilies the Pooideae or Chloridaideae.

Biotrophic fungi of the genus *Schizonella* are pathogens of the Cyperaceae (*Carex*, *Kobresia* and *Isolepis*). They are dimorphic with a saprophytic yeast stage and a parasitic mycelial stage on host plants. Sori are located on leaves forming black, short or long, pustulate streaks with an agglutinate spore mass. *Sch. caricis-atratae* is a recently described cryptic species on *Carex atrata* (PRILLINGER et al. 2009). In *Sch. cocconii* the spores are agglutinated in more or less permanent spore balls, which is a derived character. They have higher amounts of glucose in cell wall sugars (Table 3). The *Schizonella* species are classified within the order Ustilaginales, family Anthracoideaceae (Fig. 1; Denchev 1997, Begerow et al. 2006). Using cell wall sugars and ubiquinone component (CoQ) analyses, PRILLINGER et al. (1993a) showed for the first time that the genus *Melanotaenium* is heterogenous. The type species of the genus, *Melanotaenium endogenum* (a parasite on a dicot, *Galium mollugo*), a CoQ 9 species with a cell wall glucose content of 81%, belongs to the Ustilaginales (BOEKHOUT et al. 2011). On the other hand *M. ari* parasitizing a monocot, *Arum* sp., a CoQ 10 species with a higher glucose content (95%), is closely related to *Urocystis* species and is placed in the Urocystales on the basis of the phylogenetic study of Begerow (pers. comm.). Both species contain no mannose.

### Yeasts and dimorphic fungi belonging to the *Tremella*-type:

The current concept of Agaricomycotina is comprised of three classes, namely Agaricomycetes, Dacrymycetes and Tremellomycetes (MATHENY et al. 2006, HIBBETT et al. 2007, OBERWINKLER 2012 a,b). In this publication we add a fourth class the Cystofilobasidiomycetes. Yeasts and dimorphic taxa are found only in the Tremellomycetes (BOEKHOUT et al. 2011). They occur also in the Cystofilobasidiomycetes. PRILLINGER et al. (1991b, 1993a) detected a short living yeast stage in culture in the Dacrymycetes and a yeast stage in two dimorphic *Collybia* species (*C. tuberosa* PR 1986/93, *C. cookei* PR 1987/146) in the Agaricomycetes (Agaricales; PRILLINGER et al. 1993a,b, 2002). MUELLER et al. (1998) found a yeast stage from symbiotic Agaricaceae (tribe Leucocoprineae Mueller, U.G., pers. comm.) of leaf-cutting ants (*Cyphomyrmex minutus* and *C. salvini*; Fig. 1, Table 5).

**Tremellomycetes:** The taxonomy of the Tremellomycetes is shown in WEISS et al. (2014)

**Trichosporonales:** PRILLINGER et al. (2007) proposed a new genus, *Asterotremella* and a new family, Asterotremellaceae (Fig. 1) for the tremelloid yeast isolates of *Asterophora lycoperdoides* and *A. parasitica* in the *humicola* clade of the Trichosporonales. In the mixed culture of *Asterophora lycoperdoides* and the yeast *Asterotremella albida* fertile fruiting bodies appear. We interpret the yeasts of *Asterotremella albida* as sexual symbionts PRILLINGER et al. (2002, 2007). The *Asterophora/Asterotremella* system may be an ideal model to study the evolution of mating types (PRILLINGER et al. 1993b, 2002, 2007). *Asterotremella albida* is closely related to *A. humicola* (Fig. 1). Many strains

of *A. humicola* were isolated from mushrooms (FONSECA et al. 2011). BOEKHOUT et al. (2011) and WEISS et al. (2014) did not accept the genus *Asterotremella*. They suggested using the existing genus *Vanrija* MOORE for those species, since *V. humicola* (*Cryptococcus humicola*) is the type species of *Vanrija* (MOORE 1980). Therefore, from a nomenclatural point of view the use of the name *Vanrija* has priority over *Asterotremella*. MOORE (1980) suggested the genus *Vanrija* without a comprehensive English and Latin diagnosis as an anamorph for *Leucosporidium* (*V. scottii* was postulated for *L. scottii*). Based on molecular data the very speculative genus *Vanrija* is heterogenous (teleomorphs: *Leucosporidium*, *Mrakia* and probably some further genera; anamorphs: *Cryptococcus* with CoQ 9 and 10, *Mrakiella* and some further genera). In addition the name *Vanrija* does not give any information of the yeasts. The genus *Asterotremella* is phylogenetically homogenous. According to MOORE (1980) *V. humicola* is a CoQ 10 species; this is different from our results (Prillinger et al. 2007). Based on CoQ 10 we have severe doubts that Moore has the correct *C. humicola* strain in his investigations (compare SUGITA et al. 2000, TAKASHIMA et al. 2001, PRILLINGER et al. 2007). The genus *Asterotremella* is accepted from Mycobank and LIU et al. (2011). The genus *Vanrija* is not accepted from Mycobank. In the latest edition of the "The Yeasts, a Taxonomic Study" (KURTZMAN et al. 2011) neither the description of the genus *Asterotremella* nor the genus *Vanrija* exists.

**Filobasidiales:** *Christiansenia pallida* is not included in "The Yeasts, a Taxonomic Study" (Kurtzman et al. 2011). The species is studied from OBERWINKLER and BANDONI (1982). Together with *Syzygospora* and *Carcinomyces*, *Christiansenia* is placed in the Carcinomycetaceae. Cell wall sugars are available for *Carcinomyces mycetophilus* and *C. pallida* (PRILLINGER et al. 1991b). *Christiansenia pallida* is a mycoparasite on *Phanerochaeta* OBERWINKLER et al. (1984). The haustorial apparatus in *C. pallida* is similar to the haustoria in tremellaceous fungi (BAUER & OBERWINKLER 1990). The sterigmata number is unfixed 4 and 6. The sterigmata number and fucose in the cell wall are primitive characters in Carcinomycetaceae (Table 4). The phylogenetic position suggests that *C. pallida* is related to the Filobasidiales (Boekhout et al. 2011, Fig. 1). The order is accepted by OBERWINKLER (2012 a, b). EAS compounds are produced.

*Filobasidium floriforme* is the type species of the genus *Filobasidium* and the fungus was named to denote its characteristic slender, long basidia bearing basidiospores in a flower-like arrangement. EAS compounds are formed; CoQ 10 is known for *F. floriforme* (SUGIYAMA et al. 1985).

**Tremellales:** *Filobasidiella neoformans* (anamorph: *Cryptococcus neoformans*) is a human pathogenic yeast. Conjugated yeast cells produce dikaryotic hyphae with clamp connections and haustorial branches; EAS compounds are produced. Phylogenetic placement: Tremellales (KWON-CHUNG 2011, Fig. 1). CoQ 10 was found by SUGIYAMA et al. (1985). The phylogenetic tree recently constructed on the basis of ITS and D1/D2 LSU rRNA gene sequences placed the genera *Filobasidiella* and *Filobasidium* (Fig. 1 and 18S rRNA PRILLINGER et al. 2002) in two separate orders: *Filobasidiella* in the Tremellales and *Filobasidium* in the Filobasidiales (SCORZETTI et al. 2002).

*Tremella mesenterica*: According to SŁODKI et al. (1966) mannose and xylose are present as cell carbohydrates in *T. mesenterica*, *T. foliacea*, *T. encephala*, *T. brasiliensis* and *T. aurantia*. KAKUTA et al. (1979) found as cell carbohydrates fu-



cose, xylose, mannose and glucuronic acid in *T. fuciformis*. In our qualitative and quantitative analysis of cell wall sugars of *T. mesenterica* (Table 4) we found dominant amounts of glucose, mannose, xylose and small amounts of galactose. The same sugars were found in eight additional *Tremella* species. In addition small amounts of fucose were detected in *T. globispora* (PRILLINGER et al. 1991b). The genus *Tremella* is heterogenous (BANDONI & BOEKHOUT 2011). Phylogenetic placement: Tremellales (Fig. 1), Tremellaceae. EAS compounds are produced.

*Trimorphomyces papilionaceus*: The species was isolated and characterized by BANDONI & OBERWINKLER (1983). Phylogenetic placement: Tremellales (Fig. 1). EAS compounds are produced.

*Bulleromyces albus*: BANDONI (1987) reported the occurrence of mating and formation of dikaryotic hyphae with clamp connection in *Bullera*. BOEKHOUT et al. (1991) observed the formation of *Tremella*-like phragmobasidia after mating strains of *Bullera alba*. The cell carbohydrates detected by GORIN & SPENCER (1970) and von ARX & WEIJMAN (1979) agree with those of our results (Table 4). Phylogenetic placement: Tremellales (Fig. 1). EAS compounds are produced (PRILLINGER et al. 1991b).

**Cystofilobasidiomycetes** PRILLINGER & LOPANDIC, class nov. (Agaricomycotina sensu BAUER et al. 2006).

Main characteristics: dimorphic fungi, distinct clade within the Agaricomycotina (Fig. 1), teleomorphic representatives commonly with Co Q 8 (*Xanthophyllomyces* is an exception with CoQ 10), teliospores are formed, yeasts of the *Tremella*-type (urease positive, diazonium blue B positive, starch-like compounds are formed) and characteristics discussed by OBERWINKLER (2012 b) for the Cystofilobasidiales.

**Cystofilobasidiales**: *Cystofilobasidium capitatum*: The genus *Cystofilobasidium* was created by OBERWINKLER et al. (1983), who segregated *C. capitatum* and *C. bisporidii* from *Rhodospiridium* based on distinct basidial morphology. Later *C. infirmominium* was also transferred from *Rhodospiridium* to *Cystofilobasidium* (HAMAMOTO et al. 1988). The genus is placed in the order Cystofilobasidiales (SAMPAIO 2011, Fig. 1). EAS compounds are formed and CoQ 8 is present.

*Mrakia gelida*: YAMADA & KOMAGATA (1997) created the genus *Mrakia*, which consisted of four species that they transferred from *Leucosporidium*. Based on electrophoretic pattern of seven enzymes YAMADA & MATSUMOTO (1988) concluded that two species were only synonyms and accepted only *M. frigida* and *M. gelida*. MESSNER et al. (1994) using RAPD analysis and DIAZ & FELL (2000) using ITS and IGS sequence analysis confirmed the concept of YAMADA & MATSUMOTO (1988). The one-celled siphonal basidia and the presence of a high fucose content in the cell wall (table 4) suggests that *Mrakia* occupies a basal position in the Cystofilobasidiomycetes (compare PRILLINGER et al. 1991b) and the Cystofilobasidiomycetes are more primitive than the Tremellomycetes within the Agaricomycotina. CoQ 8 and EAS compounds are present. A high percentage of fucose suggests a relationship to the *Microbotryum*-type. Phylogenetic placement: Cystofilobasidiales (FELL 2011)..

*Phaffia rhodozyma* (PRILLINGER et al. 1993a) is an anamorphic yeast having a CoQ 10 in the Cystofilobasidiomycetes order Cystofilobasidiales (FELL & JOHNSON 2011)

*Atractogloea stillata* HB 260 investigated by PRILLINGER et al. (1993a, 2002) was according to Oberwinkler (pers. comm.) a tremelloid contaminant.

## Dimorphic fungi belonging to the glucose- mannose type:

**Agaricomycetes**: MUELLER et al. (1998) isolated two yeasts from symbiotic agarics (family Agaricaceae; tribe Leucocoprinae, Mueller, U. G., pers. comm.) of leaf-cutting ants (*Cyphomyrmex* species). The corresponding ITS and LSU ribosomal DNA sequences are deposited under “*Cyphomyrmex minutus* symbiont” and “*Cyphomyrmex salvini* symbiont” at Genbank (Fig. 1). The cell wall of these highly evolved agaricoid yeasts contains an extreme high amount of glucose, very low amount of mannose and no xylose, a typical sugar of the Tremellomycetes and Cystofilobasidiomycetes (Table 5). The glucose-mannose cell wall pattern is known in Ascomycota (*Saccharomyces*-type; PRILLINGER et al. 1990b, 1993a). It differs from the Basidiomycota by a negative urease test and a negative DBB test (PRILLINGER et al. 1990b, 1993a). In primitive ascomycetous yeasts with CoQ 6 mannose dominates. Cell wall sugars suggest an entomophthoralean ancestor of the ascomycetous yeasts (compare yeasts in *Entomophthora muscae* PRILLINGER 1987a; in BREFELD 1871 as *Empusa muscae*). The glucose-mannose pattern is known from cell walls of the Entomophthorales (*Entomophthora coronata*, *E. exitialis*, *E. thaxteriana* and *E. virulenta*; in *Conidiobolus stromoides* only glucose is present; (HODDINOTT & OLSON 1972, SCHWEIGKOFER et al. 2002). It seems that the glucose-mannose pattern appears at the beginning and at the end of the evolution of asco- and basidiomycetous yeasts. This fits well in the concept of phylogeny estimated by PRILLINGER et al. (2000, 2002), SCHWEIGKOFER et al. (2002) and LOPANDIC et al. (2005), where the Saccharomycotina (as Hemiascomycetes) are basal in the evolution of the Ascomycota. The subphyla Saccharomycotina, Taphrinomycotina and Pezizomycotina of the Ascomycota were introduced by ERIKSSON & WINKA (1997).

Whereas in the Pezizomycotina glucose, mannose and galactose (Ascosphaerales, Dothideales, Chaetothyriales, Hypocreales, Onygeales, Eurotiales) or glucose, mannose, galactose and rhamnose (*Ophiostoma*, *Sporothrix*, *Hyphozyma*, *Lecythophora*, *Symbiotaphrina*) dominate (SCHWEIGKOFER et al. 2002, LOPANDIC et al. 2005) the glucose and mannose pattern was found in the highly evolved ascomycete *Xylaria hypoxylon* (Xylariales; O'BRIAN & RALPH 1966).

Agaricoid yeasts were also isolated from *Collybia tuberosa* and *C. cookei* (PRILLINGER 1987b, PRILLINGER et al. 1991b, 1993b, 2000, 2002). The physiological characterization of these yeasts can be found in LAASER (1989). A small amount of xylose was found in the two *Collybia* species. A characteristic of the agaricoid yeasts is that they are not stable. The fungi grow as yeasts for a few weeks to a few months and then switch to mycelial growth. After cryopreservation at minus 130° C no growth of the yeasts occurred.

In filamentous Agaricomycetes xylose is very common: Agaricales (*Asterophora parasitica*, *Clitocybe phyllophila*, *Mycena gallopus*, *Pholiota squarrosa*), Polyporales (*Fomes fomentarius*, *Laetiporus sulfureus*, *Phanerochaete chrysosporium* and *Polyporus ciliatus*), Hymenochaetales (*Phellinus torulosus*). No xylose was found in Schizophyllales (*Schizophyllum commune*) and Boletales (*Coniophora cerebella*; O'BRIAN & RALPH 1966, PRILLINGER et al. 2002). The absence of xylose in *Schizophyllum commune* gives support to the order Schizophyllales (PRILLINGER et al. 2002).



Differently from the Basidiomycota, the cell wall sugar composition can not be used to characterize subphyla of the Ascomycota. Comparative analyses of the 18S rDNA sequences, cell wall sugars, ubiquinone data and urease activity demonstrated that the Saccharomycotina (as Hemiascomycetes) are basal and the Taphrinomycotina (as Protomycetes) and Pezizomycotina (as Euascomycetes) are sister taxa (PRILLINGER et al. 2000, 2002, SCHWEIGKOFER et al. 2002, LOPANDIC et al. 2005). Based on parasitic *Metschnikowia bicuspidata* on *Artemia salina* and *Daphnia magna* (METSCHNIKOFF 1884, LACHANCE 2011) the Saccharomycetales (glucose-mannose pattern; PRILLINGER et al. 1990b) can be traced back to more than 500 million years ago (PRILLINGER et al. 1997a). No filamentous ancestor is known for *Metschnikowia* species. This is further corroborated by the isolated position in a phylogenetic tree of complete 18S rDNA sequences (PRILLINGER et al. 2000, 2002) and by molecular data (very short ITS 1/ITS 2 sequences and an absence of nucleotides 434 to 483 in the 26S rDNA; MENDONÇA-HAGLER et al. 1993, PRILLINGER et al. 1997a). In contrast to our observations according to BERBEE & TAYLOR (1993, 2010), NISHIDA & SUGIYAMA (1994) and SUGIYAMA et al. (2006) the Saccharomycotina (Hemiascomycetes) have evolved with the Pezizomycotina (Euascomycetes) 310 million years ago. According to BERBEE & TAYLOR (1993) the genera *Kluyveromyces* and *Saccharomyces* have evolved from a filamentous ancestor 240 million years ago (compare morphological differentiation of Eumycota; (PRILLINGER 1987a, PRILLINGER et al. 1997a, 2002). The filamentous ancestor of *Saccharomyces* and *Kluyveromyces* is supported by PRILLINGER et al. (1997a).

## ACKNOWLEDGMENTS

For a first introduction in the cell wall sugar analysis we have to thank Prof. L. Lehle. For the analysis of cell wall sugars of *Malassezia furfur* we thank Dr. M. Takashima (RIKEN BioResource Center, Japan). Prof. D. Begerow informed us of the phylogenetic placement of *Melanotaenium ari* and sent us the accession number of *Microbotryum salviae*. For valuable literature we thank Prof. em. K. Esser. For critical comments we have to thank Prof. em. F. Oberwinkler. We appreciate the help of Prof. em. F. Oberwinkler, Dr. R. Bauer, Dr. U.G. Mueller, Dr. T. Boekhout, Dr. T. Nakase, Dr. G. Deml, Dr. J. Kronstad, Dr. G. Hagedorn and Prof. em. J. Sugiyama for sending interesting yeasts and dimorphic fungi. My wife Judith Prillinger and daughter Hanna Prillinger helped with correspondence and computer work. For the recommendation to publish in Stapfia we thank Prof. em. F. Oberwinkler.

## REFERENCES

- AIME M.C., MATHENY P.B., HENK D.A., FRIEDERS E.M., NILSSON R.H., PIEPENBRING M., McLAUGHLIN D.J., SZABO L.J., BEGEROW D., SAMPAIO J.B., BAUER R., WEISS M., OBERWINKLER F., HIBBETT D. (2006): An overview of the higher-level classification of Pucciniomycotina based on combined analysis of nuclear large and small subunit rDNA sequences. — *Mycologia* **98**: 896–905.
- BANDONI R.J. (1987): Taxonomic overview of the Tremellales. — *Stud. Mycol.* **30**: 87–110.
- BANDONI R.J., OBERWINKLER F. (1983): On some species of *Tremella* described by A. Möller. — *Mycologia* **75**: 854–863.
- BANDONI R.J., BOEKHOUT T. (2011): *Tremella* PERSON (1794). — In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*, 5th ed, Vol. 3. pp1567–1590. — Elsevier, Amsterdam.
- BARTNICKI-GARCIA S. (1968): Cell wall chemistry, morphogenesis and taxonomy of fungi. — *Annu. Rev. Microbiol.* **22**: 87–108.
- BAUER R., OBERWINKLER F. (1990): Haustoria of the mycoparasitic Hetero-basidiomycete *Christiansenia pallida*. — *Cytologia* **55**: 419–424.
- BAUER R., OBERWINKLER F., VÁNKY K. (1997): Ultrastructural markers and systematics in smut fungi and allied taxa. — *Can. J. Bot.* **75**: 1273–1314.
- BAUER R., BEGEROW D., NAGLER A., OBERWINKLER F. (2001a): The Georgefischeriales: a phylogenetic hypothesis. — *Mycol. Res.* **105**: 416–424.
- BAUER R., BEGEROW D., OBERWINKLER F., PIEPENBRING M., BERBEE M.L. (2001b): Ustilaginomycetes. In: McLAUGHLIN D.J., McLAUGHLIN E.G., LEMKE P.A., (eds.) *Systematics and Evolution. The Mycota VII Part B*. pp. 57–83. — Springer-Verlag, Berlin.
- BAUER R., BEGEROW D., SAMPAIO J.P., WEISS M., OBERWINKLER F. (2006): The simple-septate basidiomycetes: a synopsis. — *Mycol. Progress* **5**: 41–66.
- BEGEROW D., BAUER R., OBERWINKLER F. (1997): Phylogenetic studies on the nuclear large subunit ribosomal DNA of smut fungi and related taxa. — *Can. J. Bot.* **75**: 2045–2056.
- BEGEROW D., BAUER R., BOEKHOUT T. (2000): Phylogenetic placements of ustilagino-mycetous anamorphs as deduced from nuclear LSU rDNA sequences. — *Mycol. Res.* **104**: 53–60.
- BEGEROW D., STOLL M., BAUER R. (2006): A phylogenetic hypothesis of Ustilagino-mycotina based on multiple gene analyses and morphological data. — *Mycologia* **98**: 906–916.
- BERBEE M.L., TAYLOR J.W. (1993): Dating the evolutionary radiations of the true fungi. — *Can. J. Bot.* **71**: 1114–1127.
- BERBEE M.L., TAYLOR J.W. (2010): Dating the molecular clock in fungi – how close are we? — *Fungal Biol. Rev.* **24**: 1–16.
- BOEKHOUT T. (1991): A revision of ballistoconidia-forming yeasts and fungi. — *Stud. Mycol.* **33**: 1–194.
- BOEKHOUT T. (2011): *Tilletiopsis* DERX EX DERX (1930). In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*, 5th ed, Vol 3. pp. 2003–2014. — Elsevier, Amsterdam.
- BOEKHOUT T., FONSECA A., BATENBURG-VAN DER VEGTE W.H. (1991): *Bulleromyces* genus novum (Tremellales), a teleomorph for *Bullera alba* and the occurrence of mating in *Bullera varabilis*. — *Antonie van Leeuwenhoek* **59**: 81–93.
- BOEKHOUT T., FELL J.W., FONSECA A., PRILLINGER H., LOPANDIC K., ROEIJMANS H. (2000): The basidiomycetous yeast *Rhodotorula yarrowii* comb.nov. — *Antonie van Leeuwenhoek* **7**: 355–358.
- BOEKHOUT T., FONSECA A., SAMPAIO J.P., BANDONI R.J., FELL J.W., KWON-CHUNG K.J. (2011): Discussion of teleomorphic and anamorphic basidiomycetous yeasts. In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*, 5th ed, Vol. 3, pp 1339–1372. — Elsevier, Amsterdam.
- BREFELD O. (1871): Untersuchungen über die Entwicklung der *Empusa muscae* und *Empusa (Entomophthora) radicans* und die durch sie verursachten Epidemien der Stubenfliegen und Raupen. Abhandlungen der naturforschenden Gesellschaft in Halle — **12**: 1–50.
- COUCH J.N. (1938): *The Genus Septobasidium*. — The University of North Carolina Press. Chapel Hill. U.S.A.

- DENCHEV C.M. (1997): Anthracoideaceae, a new family in the Ustilaginales. — *Mycotaxon* **64**: 411–417.
- DERX H.G. (1930). Étude sur les Sporobolomycètes. — *Ann. Mycol.* **28**: 1–23.
- DIAZ M.R., FELL J.W. (2000): Molecular analysis of ITS and IGS rDNA regions of the psrophilic yeasts in the genus *Mrakia*. — *Antonie van Leeuwenhoek* **77**: 7–12.
- DÖRFLER C. (1990): Vergleichende Untersuchungen zum biochemischen Aufbau der Zellwand an Hefestadien von niederen und höheren Basidiomyceten. — *Bibl. Mycol.* **129**: 1–163.
- ERIKSSON O.E., WINKA K. (1997): Supraordinal taxa of Ascomycota. — *Myconet* **1**: 1–16.
- FELL J.W. (2011): *Mrakia* Y. YAMADA & KOMAGATA (1987) In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*. 5th ed., Vol 3, pp. 1503–1513. — Elsevier, Amsterdam.
- FELL J.W., JOHNSON E.A. (2011): *Phaffia* M.W. MILLER, YONEYAMA & SONEDA (1976) In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*. 5th ed., Vol 3, pp. 1853–1855. — Elsevier, Amsterdam.
- FONSECA A., BOEKHOUT T., FELL J.W. (2011): *Cryptococcus* VUILLEMIN (1901). In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*. 5th ed., Vol. 3, pp.1661–1737. — Elsevier, Amsterdam.
- GORIN P.A.J., SPENCER J.F.T. (1970): Proton magnetic resonance spectroscopy – an aid in identification and chemotaxonomy of yeasts. — *Adv. Appl. Microbiol.* **13**: 25–89.
- GOTTSCHALK M., BLANZ P.A. (1985): Untersuchungen an 5S ribosomalen Ribonucleinsäuren als Beitrag zur Klärung von Systematik und Phylogenie der Basidiomyceten. — *Z. Mycol.* **51**: 205–244.
- HAMAMOTO M. (2011): *Erythrobasidium* Hamamoto, SUGIYAMA & KOMAGATA (1991). In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts A Taxonomic Study*, 5th ed., Vol. 3, pp. 1433–1435, — Elsevier, Amsterdam.
- HAMAMOTO M., SUGIYAMA J., KOMAGATA K. (1988): Transfer of *Rhodosporeidium infirmominiatum* to the genus *Cystofilobasidium* as *Cystofilobasidium infirmominiatum* comb. nov. — *J. Gen. Appl. Microbiol.* **34**: 271–278.
- HAMAMOTO M., NAKASE T. (2000): Phylogenetic relationships among fungi inferred from small subunit ribosomal RNA gene sequence. In: PRIEST F.G., GOODFELLOW M. (eds.) *Applied Microbial Systematics*, pp. 57–71. — Kluwer Academic Publishers, The Netherlands.
- HAMAMOTO M., BOEKHOUT T., NAKASE T. (2011): *Sporobolomyces* KLUYVER & VAN NIEL (1924). In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*, 5th ed., Vol 3, pp. 1929–1990. — Elsevier, Amsterdam.
- HIBBETT D.S., BINDER M., BISCHOFF J.F., BLACKWELL M., CANNON P.F., ERIKSSON O.E., HUHDORF S., JAMES T., KIRK P.M., LÜCKING R., LUMBSCH H.T., LUTZONI F., MATHENY P.B., McLAUGHLIN D.J., POWELL M.J., REDHEAD S., SCHOCH C.L., SPATAFORA J.W., STALPERS J.A., VILGALYS R., AIME M.C., APTROOT A., BAUER R., BEGEROW D., BENNY G.L., CASTLEBURY L.A., CROUS P.W., DAI Y.-C., GAMS W., GEISER D.M., GRIFFITH G.W., GUEIDAN C., HAWKSWORTH D.L., HESTMARK G., HOSAKA K., HUMBER R.A., HYDE K.D., IRONSIDE J.E., KOLJALG U., KURTZMAN C.P., LARSSON K.-H., LICHTWARDT R., LONGCORE J., MIADLIKOWSKA J., MILLER A., MONCALVO J.-M., MOZLEY-STANDRIDGE S., OBERWINKLER F., PARMASO E., REEB V., ROGERS J.D., ROUX C., RYVARDEN L., SAMPAIO J.P., SCHÜSSLER A., SUGIYAMA J., THORN R.G., TIBELL L., UNTEREINER W.A., WALKER C., WANG Z., WEIR A., WEISS M., WHITE M.M., WINKA K., YAO Y-J, ZHANG N. 2007. A higher-level phylogenetic classification of the Fungi. — *Mycol. Res.* **111**: 509–547.
- HODDINOTT J., OLSON O. (1972): A study of the carbohydrates in the cell walls of some species of the Entomophthorales. — *Can. J. Bot.* **50**: 1675–1679.
- KAKUTA M., SONE Y., UMEDA T., MISAKI A. (1979): Comparative structural studies on acidic heteropolysaccharides isolated from “Shirokikurage”, fruitbody of *Tremella fuciformis* Berk. and the growing culture of its yeast-like cells. — *Agric. Biol. Chem.* **43**: 1659–1668.
- KURTZMAN C.P., FELL J.W., BOEKHOUT T. (2011): *The Yeasts, A Taxonomic Study*, 5th ed., Vol. 3, pp. 1339–2080. — Elsevier, Amsterdam.
- KWON-CHUNG K.J. (2011): *Filobasidiella* KWON-CHUNG (1975) In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*. 5th ed., Vol 3, pp. 1443–1455, — Elsevier, Amsterdam.
- LAASER G. (1989): Vergleichende systematische Studien an Basidiomycetenhefen unter besonderer Berücksichtigung der Hefestadien. — *Bibl. Mycol.* **130**: 1–325.
- LACHANCE M.-A. (2011): *Metschnikowia* KAMIENSKI (1899) In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*, 5th ed., Vol 2, pp. 575–620 — Elsevier, Amsterdam.
- LIU Y.-R., HUANG L.-Y., YOUNG S.-S., CHANG C.-F., LEE C.-F. (2011): *Asterotremella meifongana* sp. nov. and *Asterotremella nantouana* sp. nov., two anamorphic basidiomycetous yeasts isolated from soil and mushrooms. — *Antonie van Leeuwenhoek* **99**: 643–650.
- LOPANDIC K., MOLNÁR O., SUZUKI M., PINSKER W., PRILLINGER H. (2005): Estimation of phylogenetic relationships within the Ascomycota on the basis of 18S rDNA sequences and chemotaxonomy. — *Mycol Progress* **4**: 205–214.
- MATHENY P.B., CURTIS J.M., HOFSTETTER V., AIME M.C., MONCALVO J.M., GE Z.W., SLOT J.C., AMMIRATI J.F., BARONI T.J., BOUGHER N.L., HUGHES K.W., LODGE D.J., KERRIGAN R.W., SEIDL M.T., AANEN D.K., DENITIS M., DANIELE G.M., DESJARDIN D.E., KROPP B.R., NORVELL L.L., PARKER A., VELLINGA E.C., VILGALYS R., HIBBETT D.S. (2006): Major clades of Agaricales: a multilocus phylogenetic overview. — *Mycologia* **98**: 982–985.
- MENDONÇA-HAGLER L.C., HAGLER A.N., KURTZMAN C.P. (1993): Phylogeny of *Metschnikowia* species estimated from partial rRNA sequences. — *Int. J. Syst. Bacteriol.* **43**: 368–373.
- MESSNER R., PRILLINGER H., ALTMANN F., LOPANDIC K., WIMMER K., MOLNÁR O., WEIGANG F. (1994): Molecular characterization and application of random amplified polymorphic DNA analysis of *Mrakia* and *Sterigmatomyces*. — *Int. J. Syst. Bacteriol.* **44**: 694–703.
- METSCHNIKOFF E. (1884): Über eine Sproßpilzkrankheit der Daphnien. Beitrag zur Lehre über den Kampf der Phagocyten gegen Krankheitserreger. — *Arch. Pathol. Anat. Physiol.* **96**: 177–195.
- MOORE RT. (1980): Taxonomic proposals for the classification of marine yeasts and other yeast-like fungi including the smuts. — *Bot. Mar.* **23**: 361–373.
- MUELLER U.G., REHNER S.A., SCHULTZ T.R. (1998): The evolution of agriculture in ants. — *Science* **281**: 2034–2038.
- NISHIDA H., SUGIYAMA J. (1994): Archiascomycetes: detection of a major new lineage within the Ascomycota. — *Mycoscience* **35**: 361–366.
- NISHIDA H., ANDO K., ANDO Y., HIRATA A., SUGIYAMA J. (1995): *Mixia osmundae*: transfer from the Ascomycota to the Basidiomycota based on evidence from molecules and morphology. — *Can. J. Bot.* **73**: S660–S666.
- NISHIDA H., ROBERT V., SUGIYAMA J. (2011): *Mixia* C.L. KRAMER EMEND. H. NISHIDA, K. ANDO, Y. ANDO, HIRATA & SUGIYAMA (1995). In: KURTZMAN C.P., FELL J.W., BOEKHOUT T. (eds.) *The Yeasts, A Taxonomic Study*. 5th ed., Vol 3, pp. 1499–1502. — Elsevier, Amsterdam.

- OBERWINKLER F. (1977): Das neue System der Basidiomyceten. In: FREY W., HURKA H., OBERWINKLER F., (eds.). Beiträge zur Biologie der Niederen Pflanzen, pp 59–105. — Fischer-Verlag, Stuttgart.
- OBERWINKLER F. (2012 a): Evolutionary trends in Basidiomycota. — *Stapfia* **96**: 45–104.
- OBERWINKLER F. (2012 b): Mykologie am Lehrstuhl Spezielle Botanik und Mykologie der Universität Tübingen, 1974–2011. — *Andrias* **19**: 23–110.
- OBERWINKLER F., BANDONI R.J. (1982): Carcinomycetaceae: a new family in the Heterobasidiomycetes. — *Nord. J. Bot.* **2**: 501–516.
- OBERWINKLER F., BANDONI R.J., BLANZ P., DEML G., KISIMOVA-HOROWITZ L. (1982): Graphioidales: basidiomycetes parasitic on palms. — *Plant Syst. Evol.* **140**: 251–277.
- OBERWINKLER F., BANDONI R.J., BLANZ P., KISIMOVA-HOROWITZ L. (1983): *Cystofilobasidium* a new genus in the Filobasidiaceae. — *Syst. Appl. Microbiol.* **4**: 114–122.
- OBERWINKLER F., BANDONI R.J., BAUER R., DEML G., KISIMOVA-HOROWITZ L. (1984): The life-history of *Christiansenia pallida*, a dimorphic mycoparasitic heterobasidiomycete. — *Mycologia* **76**: 9–22.
- OBERWINKLER F., BAUER R., BANDONI R.J. (1990): *Colacogloea*: a new genus in the auriculagarioid Heterobasidiomycetes. — *Can. J. Bot.* **68**: 2531–2536.
- O'BRIEN R.W., RALPH B.J. (1966): The cell wall composition and taxonomy of some Basidiomycetes and Ascomycetes. — *Ann. Bot. NS.* **30**: 831–843.
- PRILLINGER H. (1987a). Yeasts and anastomoses: their occurrence and implications for the phylogeny of Eumycota. In: RAYNER A.D.M., BRASIER C.M., MOORE D., (eds.). *Evolutionary Biology of the Fungi*. pp.355–377. — Cambridge University Press, New York.
- PRILLINGER H. (1987b). Are there yeasts in Homobasidiomycetes? — *Stud. Mycol.* **30**: 33–59.
- PRILLINGER H., DÖRFLER C., LAASER G., HAUSKA G. (1990a): Ein Beitrag zur Systematik und Entwicklungsbiologie höherer Pilze. Hefetypen der Basidiomyceten. Teil III: *Ustilago*-Typ. — *Z. Mykol.* **56**: 251–278.
- PRILLINGER H., DÖRFLER C., LAASER G., ECKERLEIN B., LEHLE L. (1990b): Ein Beitrag zur Systematik und Entwicklungsbiologie höherer Pilze. Hefetypen der Basidiomyceten. Teil I: Schizosaccharomyceales, *Protomyces*-Typ. — *Z. Mykol.* **56**: 219–250.
- PRILLINGER H., DEML G., DÖRFLER C., LAASER G., LOCKAU W. (1991a): Ein Beitrag zur Systematik und Entwicklungsbiologie höherer Pilze. Hefetypen der Basidiomyceten. Teil II: *Microbotryum*-Typ. — *Bot. Acta.* **104**: 5–17.
- PRILLINGER H., LAASER G., DÖRFLER C., ZIEGLER K. (1991b): Ein Beitrag zur Systematik und Entwicklungsbiologie höherer Pilze. Hefetypen der Basidiomyceten Teil IV: *Dacrymyces*-Typ, *Tremella*-Typ. — *Sydowia* **53**: 170–218.
- PRILLINGER H., OBERWINKLER F., UMILE C., TLACHAC K., BAUER R., DÖRFLER C., TAUFRAITZHOFFER E. (1993a): Analysis of cell wall carbohydrates (neutral sugars) from ascomycetous and basidiocetous yeasts with and without derivatization. — *J. Gen. Appl. Microbiol.* **39**: 1–34.
- PRILLINGER H., ALTENBUCHNER J., LAASER G., DÖRFLER C. (1993b): Yeasts isolated from homobasidiomycetes (*Asterophora*, *Collybia*): new aspects for sexuality, taxonomy, and speciation. — *Exp. Mycol.* **17**: 24–45.
- PRILLINGER H., SCHWEIGKOFER W., BREITENBACH M., BRIZA P., STAUDACHER E., LOPANDIC K., MOLNÁR O., WEIGANG F., IBL M., ELLINGER A. (1997a): Phytopathogenic filamentous (*Ashbya*, *Eremothecium*) and dimorphic fungi (*Holleya*, *Nematospora*) with needle-shaped ascospores as new members within the Saccharomycetaceae. — *Yeast* **13**: 945–960.
- PRILLINGER H., KRAEPELIN G., LOPANDIC K., SCHWEIGKOFER W., MOLNÁR O., WEIGANG F., DREYFUSS M.M. (1997b). New species of *Fellomyces* isolated from epiphytic lichen species. — *Syst. Appl. Microbiol.* **20**: 572–584.
- PRILLINGER H., LOPANDIC K., SCHWEIGKOFER W., STERFLINGER K. (2000): Molecular phylogeny and systematics of the fungi with special reference to the Asco- and Basidiomycota. The 20th Annual meeting on microbial systematics, Microbial Systematics, Today and Tomorrow, pp.5–14. — The University of Tokyo. At Sanjo Kaikan, Hongo.
- PRILLINGER H., LOPANDIC K., SCHWEIGKOFER W., DEAK R., AARTS H.J.M., BAUER R., STERFLINGER K., KRAUS G.F., MARAZ A. (2002): Phylogeny and systematic of the Fungi with special reference to the Ascomycota and Basidiomycota. In: BREITENBACH M., CRAMER R., LEHRER S.B. (eds.). *Fungal Allergy and Pathogenicity*. Chem. Immunol. **81**, pp 207–295, — Karger, Basel.
- PRILLINGER H., LOPANDIC K., STERFLINGER K., METZGER E., BAUER R. (2003): Hefen gestern und heute. — *Science Week Austria*, 2–13.
- PRILLINGER H., LOPANDIC K., SUGITA T., WUCKOWSKI M. (2007): *Asterotremella* gen. nov. *albida*, an anamorphic tremelloid yeast isolated from the agarics *Asterophora lycoperdoides* and *A. parasitica*. — *J. Gen. Appl. Microbiol.* **53**: 167–175.
- PRILLINGER H., WUCZKOWSKY M., LOPANDIC K., BAUER R., MOLNÁR O., STERFLINGER K. (2009): *Schizonella caricis-atratae* (Ustilaginomycetes): a new cryptic species on *Carex atrata* from Austria. — *Mycol. Progress.* **8**: 157–164.
- PRILLINGER H., LOPANDIC K., SUZUKI M., KOCK J.L.F., BOEKHOUT T. (2011): Chemotaxonomy of Yeasts. In: KURTZMAN C.P., FELL J.W., BOEKHOUT T., (eds.) *The Yeasts, A Taxonomic Study*, 5th ed., Vol. 1, pp. 129–136. — Elsevier, Amsterdam.
- SAMPAIO J.P. (2011): *Cystofilobasidium* OBERWINKLER & BANDONI (1983) In: KURTZMAN C.P., FELL J.W., BOEKHOUT T., (eds.) *The Yeasts, A Taxonomic Study*, 5th ed., Vol. 3, pp. 1423–1432. — Elsevier, Amsterdam.
- SAMPAIO J.P., OBERWINKLER F. (2011a): *Occultifur* OBERWINKLER (1990). In: KURTZMAN C.P., FELL J.W., BOEKHOUT T., (eds.) *The Yeasts, A Taxonomic Study*, 5th ed., Vol. 3, pp. 1515–1518. — Elsevier, Amsterdam.
- SAMPAIO J.P., OBERWINKLER F. (2011b): *Kriegeria* BRESADOLA (1891) In: KURTZMAN C.P., FELL J.W., BOEKHOUT T., (eds.) *The Yeasts, A Taxonomic Study*. 5th ed., Vol 3, pp. 1477–1479. — Elsevier, Amsterdam.
- SAVILE D.B.O. (1955): A phylogeny of the basidiomycetes. — *Can. J. Bot.* **33**: 60–103.
- SCHWEIGKOFER W., LOPANDIC K., MOLNÁR O., PRILLINGER H. (2002): Analysis of phylogenetic relationships among Ascomycota with yeast phases using ribosomal DNA sequences and cell wall sugars. — *Org. Divers. Evol.* **2**: 1–17.
- SCORZETTI G., FELL J.W., FONSECA A., STATZELL-TALLMAN A. (2002): Systematics of basidiomycetous yeasts: a comparison of large sub-unit D1D2 and internal transcribed spacer rDNA regions. — *FEMS Yeast Res.* **2**: 495–517.
- SŁODKI M.E., WICKERHAM L.J., BANDONI R.J.. (1966): Extracellular heteropolysaccharides from *Cryptococcus* and *Tremella*: a possible taxonomic relationship. — *Can. J. Microbiol.* **12**: 489–494.
- STOLL M., PIEPENBRING M., BEGEROW D., OBERWINKLER F. (2003): Molecular phylogeny of *Ustilago* and *Sporisorium* species (Basidiomycota, Ustilaginales) based on internal transcribed spacer (ITS) sequences. — *Can. J. Bot.* **81**: 976–984.
- STOLL M., BEGEROW D., OBERWINKLER F. (2005): Molecular phylogeny of *Ustilago*, *Sporisorium* and related taxa based on combined analysis of rDNA sequences. — *Mycol. Res.* **109**: 342–356.



- SUGITA T., TAKASHIMA M., IKEDA R., NAKASE T., SHINODA T. (2000): Phylogenetic and taxonomic heterogeneity of *Cryptococcus humicola* by analysis of the sequences of the internal transcribed spacer regions and 18S rDNA, and the phylogenetic relationships of *C. humicola*, *C. curvatus* and the genus *Trichosporon*. — *Microbiol. Immunol.* **44**: 455–461.
- SUGIYAMA J., FUKAGAWA M., CHIU S.-W., KOMAGATA K. (1985): Cellular carbohydrate composition, DNA base composition, ubiquinone system and diazonium blue B color test in the genera *Rhodospiridium*, *Leucosporidium*, *Rhodotorula* and related basidiomycetous yeasts. — *J. Gen. Appl. Microbiol.* **31**: 519–550.
- SUGIYAMA J., HOSAKA K., SUH S.-O. (2006): Early diverging Ascomycota: phylogenetic divergence and related evolutionary enigmas. — *Mycologia* **98**: 996–1005.
- SWANN E.C., TAYLOR J.W. (1993): Higher taxa of Basidiomycetes: an 18S rRNA gene perspective. — *Mycologia* **85**: 923–936.
- SWANN E.C., TAYLOR J.W. (1995): Phylogenetic diversity of yeast-producing basidiomycetes. — *Mycol. Res.* **99**: 1205–1210.
- TAKASHIMA M., HAMAMOTO M., NAKASE T. (2000): Taxonomic significance of fucose in the class Urediniomycetes: distribution of fucose in cell wall and phylogeny of urediniomycetous yeasts. — *System. Appl. Microbiol.* **23**: 63–70.
- TAKASHIMA M., SUGITA T., SHINODA T., NAKASE T. (2001): Reclassification of the *Cryptococcus humicola* complex. — *Int. J. Syst. Evol. Microbiol.* **51**: 2199–2210.
- THOMPSON J.D., GIBSON T.J., PLEWNIK F., JEANMOUGIN F., HIGGINS D.G. (1997): The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. — *Nucleic Acids Res.* **25**: 4876–4882.
- TOOME M., ROBERSON R.W., AIME M.C. (2013): *Meredithblackwellia eburnea* gen. et sp. nov., Kriegeriaceae fam. nov. and Kriegeriales ord. nov. — toward resolving higher-level classification in Microbotryomycetes. — *Mycologia* **105**: 485–495.
- VAN DE PEER Y., DE WACHTER R. (1994): TREECON for Windows: a software package for the construction and drawing of evolutionary trees for the Microsoft Windows environment. — *Comput. Appl. Biosci.* **10**: 569–570.
- VÁNKY K. (1987): Illustrated genera of smut fungi. Cryptogamic studies Vol I, — Gustav Fischer Verlag, Stuttgart.
- VÁNKY K. (1994): European smut fungi. — Gustav Fischer Verlag, Stuttgart.
- VON ARX J.A., WEJMAN A.C.M. (1979): Conidiation and carbohydrate composition in some *Candida* and *Torulopsis* species. — *Antonie van Leeuwenhoek* **45**: 547–555.
- WEISS M., BAUER R., SAMPAIO J.P., OBERWINKLER F. (2014): Tremellomycetes and related groups. In: ESSER K. (ed.) *The Mycota. Vol. VII, Systematics and Evolution. Part A*, 2nd. ed. McLAUGHLIN D.J., SPATAFORA J.W. Vol. (eds.) pp. 331–355. — Springer, Heidelberg, Germany.
- YAMADA Y., KOMAGATA K. (1987): *Mrakia* gen. nov., a heterobasidiomycetous yeast genus for the Q8-equipped, self-sporulating organisms which produce a unicellular metabasidium, formerly classified in the genus *Leucosporidium*. — *J. Gen. Appl. Microbiol.* **33**: 455–457.
- YAMADA Y., MATSUMOTO A. (1988): An electrophoretic comparison of enzymes in strains of species in the genus *Mrakia* YAMADA & KOMAGATA (Filobasidiaceae). — *J. Gen. Appl. Microbiol.* **34**: 201–208.
- YAMADA Y., NAKAGAWA Y., BANNO I. (1989): The phylogenetic relationship of the Q9-equipped species of the heterobasidiomycetous yeast genera *Rhodospiridium* and *Leucosporidium* based on the partial sequencing of 18S and 26S ribosomal ribonucleic acids: the proposal of a new genus *Kondoa*. — *J. Gen. Appl. Microbiol.* **35**: 377–385.
- YURKOW A., KACHALKIN A., DANIEL H.-M., GROENEWALD M., LIBKIND D., DE GARCIA V., ZALAR P., GOULIAMOVA D.E., BOEKHOUT T., BEGEROW D. (2015): Two yeast species *Cystobasidium psychroaquaticum* f.a. sp. nov. and *Cystobasidium rietchieii* f.a. sp. nov. isolated from natural environments, and the transfer of members of *Rhodotorula minuta* clade to the genus *Cystobasidium*. — *Antonie van Leeuwenhoek* **107**: 173–185.